Introduction to plant virology

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L. Bos

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Preface

This book has been written for prospective and practising plant pathologists and biologists, and for workers involved in plant protection. Scientific knowledge on plant viruses is rapidly increasing, but practical information is often lacking.

There are a couple of excellent thick textbooks dealing with plant viruses, but they are too expensive for non-specialists and for most students, especially in developing countries. They also go into great detail about the special nature of viruses rather than about their involvement in crop production.

The present text should fill a gap by outlining the fundamentals of plant viruses and of their control. It emphasizes ecological aspects and shows how human interference with nature can prevent virus diseases but can sometimes encourage them.

This publication has resulted from various activities. My main work is to support Dutch farming with research on applied plant virology at the Research Institute for Plant Protection at Wageningen. Sometimes I teach in courses for technical officers of the Netherlands Agricultural and Horticultural Advisory Services and of the Plant Protection Service. I have sometimes acted as a consultant for FAO on plant virology and for some international institutes for agricultural research in developing countries, sponsored by the Consultative Group on International Agricultural Research. The book reflects my personal engagement in a fascinating and scientifically rewarding field of study that has considerable consequence for human society.

I am much indebted to Mr J. C. Rigg, Pudoc, Wageningen, for careful editing, help with the English, and detailed discussions on linguistic, terminological and technical aspects, to Mr R. J. P. Aalpol for technical editing, and to Dr D. Peters, Department of Virology, Agricultural University, Wageningen, for critical comments on Chapters 5 and 7 dealing with molecular biology of viruses. A number of virologists have kindly supplied photographs and publishers have given permission to reproduce figures.

The text will certainly not be perfect in presentation and precision of data. I would therefore greatly appreciate the readers' lenience in judgment, their kindness in informing me of whatever errors they may encounter and of any comment that may help me to improve the text.

Wageningen, July 1982 L. Bos

1 Introduction

An ever-increasing number of ailments of man, animal and plant are ascribed to viruses. They are the subject of intensive research. But the virus is still shrouded in mystery for most people. So diseases of uncertain cause are readily attributed to 'a virus' and several virus diseases are still attributed to a range of other causes.

Viruses are now known to be pathogens far different from parasitic micro-organisms. Molecular biology, soaring high in recent decennia, is trying to elucidate the biological functions of normal cell constituents and of viruses from their molecular structures. This field of study has provided spectacular techniques, such as ultra-centrifuging and electron microscopy, which have helped us in manipulating and seeing many mysterious viruses. These studies have thrown new light on the riddle of life.

Plant viruses are not only interesting tools of research on molecular biology. They play a major role in nature, though far from fully understood. They were first detected as growth-reducing factors in agriculture, and most research on them is still in agricultural institutions.

So far, some 650 have been described to some degree, but nature undoubtedly has many more in store. In wild plants and in crops, viruses are often hard to detect. Some infect many of their hosts without producing overt symptoms. Others produce symptoms closely resembling physiological disorders (such as mineral deficiencies) or genetic deviations. Viruses are certainly much more important than is so far known. In fact, viruses are multifarious in their effects on plants. Because most viruses are highly contagious, infections in crops may rapidly attain epidemic proportions and they do so especially under modern agriculture with uniform crops. Hence viruses are being increasingly recognized as major constraints to crop improvement.

Besides interfering with crop production, plant viruses have associations with various elements of the environment, especially living elements such as wild plants, that may act as sources of infection, and insects, nematodes and fungi, which may act as vehicles of spread. Such associations are highly interesting from an ecological point of view. Their study is essential to explain the often erratic nature of virus epidemics.

The main line of thought in working out the structure of this book was to emphasize viruses as factors harmful to plants, thus to describe their pathogenic relationships with plants and crops and to indicate what can be done to protect crops from adverse effects of viruses.

This explains why the book starts with three chapters on the biology of plant viruses. These chapters also follow the historical development of virology. Chapter 2 will sketch how viruses were detected and this will demonstrate how and why they are unique pathogens requiring special techniques of study. Chapter 3 will deal with viruses as disease incitants and 4 with how they are contagious agents and get from one plant to another.

Four chapters then provide information on the viruses themselves with emphasis on their physical chemistry. Some detail will be essential to appreciate their role in nature and their diversity. Chapter 5 describes the viruses as macromolecules, explaining how they can be isolated and handled for further study. Chapter 6 discusses some characteristics of viruses as physical particles, as studied by serology and electron microscopy. Chapter 7 characterizes viruses as packages of genetic information and explains how they interfere with their hosts. Chapter 8, on order out of chaos, outlines their description, classification, naming and associated aspects.

The last two major chapters return to the role of plant viruses in nature and agriculture and to what can be done about them. Chapter 9 describes the ecology of viruses diseases and how epidemics may build up. Chapter 10 surveys measures for crop protection against viruses and discusses the organizations needed to gather and disseminate information on plant viruses to help farmers to make protection of their crops against viruses effective.

An epilogue (Chapter 11) places the information on plant viruses and human involvement in a philosophical perspective.

The references at the end of each chapter are limited to a few publications of special historic interest and to some reviews of literature, preferably in English, for further reading. Reference works are listed in a separate section (Appendix B) at the end of the book. Names and Groups of plant viruses are listed in Appendix A. Leaf it through before you start on Chapter 2, though you will not fully appreciate its content until you have studied Chapters 5 to 8.

2 From virus discovery to virology

Little by little an awareness emerged that not all plant pathogens are living organisms. Likewise, the definition of a virus has gradually evolved and is still developing. The recent detection of mycoplasmas as important plant pathogens and their distinction from viruses has shown the incompleteness of long prevailing definitions of virus and the chances that many so-called virus diseases may eventually turn out to have other incitants. A brief historical outline may help to elucidate the uniqueness of viruses.

Shortcomings of microbiology

Towards the end of the Nineteenth Century, Pasteur and Koch associated infectious diseases with micro-organisms, microbes, or (light) microscopically visible forms of life, popularly known as 'disease germs'. In the wake of their discovery, many diseases of man, animals and plants could be attributed to micro-organisms. Most were bacteria and fungi. Knowledge of them enormously increased after the discovery that they could be cultured and isolated in 'pure culture' on or in artificial substrates, and be further studied outside their natural hosts. This technique marked the beginning of microbiology.

Koch's postulates, in the vogue since about 1880 are still considered essential to reliable diagnosis of infectious diseases. They state that to establish a micro-organism as the cause of a disease:

1. it must be found in all cases of the disease
2. it must be isolated from the host and grown in pure culture
3. it must reproduce the original disease when re-introduced into a susceptible host
4. it must be found in the experimental host so infected.

Application of these postulates shed light on the nature of various diseases and greatly assisted in their distinction. Order thus began to emerge in the study of contagious diseases.

Koch's postulates soon appeared to be an oversimplification. Several bacteria and fungi had special requirements and failed to grow outside their natural hosts. But more important, several contagious diseases had long been known, though their incitants could not be seen, isolated nor cultured.

The oldest known example is of flower colour-breaking in tulip (Plate 1) splendidly depicted in many Dutch still lifes, painted during the early part of the 17th Century. The phenomenon was first described at Leyden by Clusius (de l'Ecluse) in 1576, 16 years after the introduction of tulips into the Netherlands from the Middle East. Patterns of colour-breaking were so attractive that the value of single bulbs producing a 'broken' tulip flower soared to fortunes. Around 1637, the gambling trade suddenly collapsed, perhaps because some bulb growers had learnt how to transmit the abnormality to healthy plants by tuber grafting, as apparent from a document of 1643.

Another example is leaf variegation in woody ornamentals. Best known are the attractively variegated plants of *Abutilon striatum* var. *spurium* often known as var. *thompsonii* (Plate 2). The variety was imported into Europe in 1868 as an indoor ornamental an[illegible], [illegible]n found to be only perpetuated by vegetative propagation. In 1869, Lemoine in France and Morren in Belgium discovered independently that the phenomenon was graft-transmissible and thus infectious. In fact, there are earlier English reports of possibly related graft-transmissible abnormalities, demonstrating 'action of scion on stock' and on new growth.

Other diseases of mysterious cause long ascribed to mere physiological ageing of cultivars and to 'unnatural' vegetative propagation were 'degeneration diseases' of potato known in Europe since the 18th Century. New cultivars bred from seed were first vigorous and looked healthy.

Virus discovery

A breakthrough was made by Adolf Eduard Mayer (Fig. 1, left), Professor at the Agricultural College and Director of its Agricultural Experiment Station at Wageningen, the Netherlands, soon after their establishment in 1876. Tobacco was then an important crop in the district, and a mysterious and highly contagious disorder, which he called *mosaic disease* (Plate 4), was causing much concern. He made detailed studies but soon (1882 and 1886) reported that the disease was neither due

Fig. 1. Biologists at the cradle of plant virology. From left to right: Adolf E. Mayer, the Netherlands (1843–1942), Dimitrij Ivanovskij, Russia (1864–1920), Martinus W. Beijerinck, the Netherlands (1851–1931).

to a micro-organism nor to nutritional imbalance, though contagious as proved by artificial transmission through injection of sap from diseased plants with capillary glass needles. As early as 1882, he already speculated on the existence of a 'soluble, possibly enzyme-like contagion, although almost any analogy for such a supposition is failing in science'.

At that time, Dr Martinus Willem Beijerinck (Fig. 1, right) was teacher in botany at the Wageningen College. Immediately after becoming Professor of Microbiology at the Technical University in Delft in 1895, he tackled the problem of tobacco mosaic and soon discovered that its incitant could pass through a porcelain Chamberland filter retaining bacteria. He was unaware of similar results already obtained in Russia and published in 1892 by Dimitrij Ivanovskij (Fig. 1, middle), who claimed, however, to be dealing with a microbe. Beijerinck deserves credit for first realizing that the contagion differed essentially from micro-organisms, as indicated by his description *contagium vivum fluidum*. In 1903, Ivanovskij correctly stated the lack of evidence for the fluidous nature of the filterable pathogen, but overclaimed that it multiplied in agar.

The term virus had long been used for any slimy liquid, poison, venom or infectious matter. The new pathogen was therefore first called *filtrable virus*. Gradually *virus* acquired its modern restricted sense. The original meaning can still be detected in the commonly used adjective *virulent* for 'extremely poisonous, venomous or malignant', as of pathogens in general.

The number of known virus diseases has increased rapidly since 1920. They were mostly called mosaic diseases, because most attention was on diseases resembling tobacco mosaic, although differing in natural hosts and obvious sources of infection. Criteria for their distinction as virus diseases were:
- their infectious nature
- presumed, evident or proven submicroscopic nature
- failure of cultivation in vitro.

The true nature of viruses remained obscure despite endeavours since 1927 to include so-called physico-chemical properties in their characterization as determined in expressed plant sap by studying persistence of infectivity in such sap after:
- stepwise dilution
- heat treatment for 10 minutes at various temperatures
- ageing at room temperature
- treatment with certain chemicals.

Hence proper distinction of virus diseases remained difficult.

A new landmark was reached in 1935 when the Nobel prizewinner Wendell M. Stanley in the United States isolated a proteinaceous crystalline substance from mosaic-diseased tobacco plants. The substance remained highly infectious, even after repeated recrystallization. One year later, Bawden and Pirie in Britain chemically characterized the isolated material as a *nucleoprotein*. This success was soon followed by the first visual observation in Germany by Kausche, Pfankuch